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**Review article**

# Physiology as a caste-defining feature

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**Abstract.** Division of labour is a key factor in the ecological success of social insects. Groups of individuals specializing on a particular behaviour are known as castes and are usually distinguished by morphology or age. Physiology plays a key role in both these types of caste, in either the developmental physiology which determines morphology, or the temporal changes in physiology over an insect's life. Physiological correlates of morphological or temporal caste include differences in gland structure, secretory products, leanness, neuroanatomy and neurochemistry. However, purely physiological castes could also occur. Physiological castes are discrete groups of same-age same-size individuals with particular physiological competencies, or groups of individuals with similar physiology crossing age or size groups. A stable physiological caste occurs in the monomorphic Pharaoh's ant, where some ants can detect old pheromone trails and retain this specialization over time. These ants differ physiologically from other workers, and the differences arise before eclosion. More temporary physiological castes occur in the ant *Ectatomma* where brood care specialists have more developed ovarioles than other same-aged workers, and in the honeybee where nurses, wax-workers and soldiers all differ physiologically from same-aged nestmates. Physiology is an important aspect of caste, not only in its contribution to age-related and morphological castes, but also in its own right as a caste grouping factor. While age and morphological differences make caste structures accessible for study, more cryptic physiological castes may play just as important a role in division of labour.

*Keywords:* Caste, division of labour, physiology, social insects, polyethism.

## Introduction

Division of labour is considered a key factor in the ecological success of social insects. Reproductive division of labour is characteristic of eusocial species, but in the social insects, further division of labour among the workers increases the efficiency of task performance by allowing parallel task processing and specialisation on particular tasks such as foraging, defence or brood care. Groups of individuals that contribute to specific colony functions are known as castes, and caste differences are accompanied by distinct behavioural specializations (Oster and Wilson, 1978). Beyond that, castes are usually distinguished by morphological features of the exoskeleton, or grouped by age. A third type of caste is occasionally mentioned, the physiological caste, based on physiological differences not linked to morphology or age (Wilson, 1963; Hölldobler and Wilson, 1990). However, no examples of such a caste are given, and age and morphology are often listed as the only two types of caste (Wilson, 1968, 1980; Traniello and Rosengaus, 1997; Beshers et al., 1999).

Differences between individuals which cannot be attributed to age or morphological differences have been classed simply as 'idiosyncrasies' (Beshers et al., 1999) but it is possible that many species have physiological castes – discrete groups of same-age same-size individuals with particular physiological competencies and behavioural specialisations, or groups of individuals with similar physiology and behaviour crossing age or size groups. Such groups could easily be overlooked. Morphological castes are, after all, determined by developmental physiology (Nijhout and Wheeler, 1982), and temporal castes can be considered to be temporary physiological castes (Johnson, 2003), so morphological and age-related castes could be seen as particular subtypes of physiological caste. Rather than focussing on morphological or temporal groupings and then looking

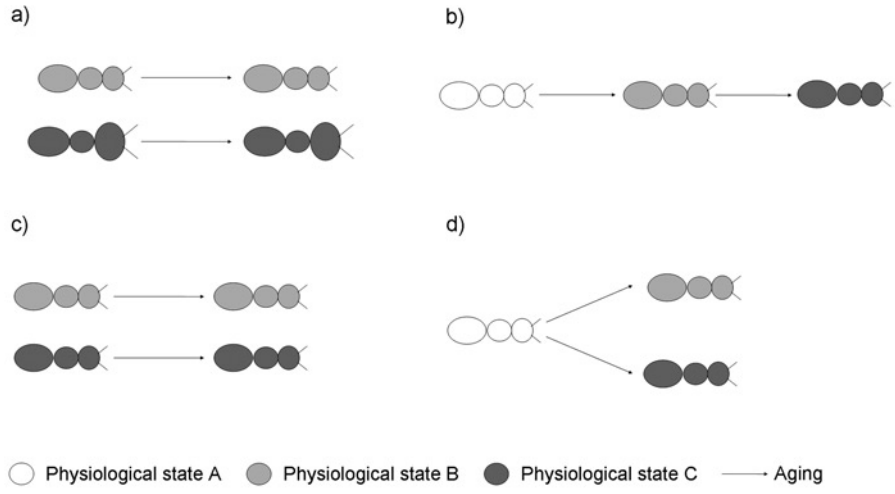


**Figure 1.** Schematic of the different types of physiological caste. **a.** Two morphological castes, each accompanied by physiological differences maintained over time, e.g. *Atta cephalotes.* **b.** Three temporal castes accompanied by physiological changes, e.g. *Myrmica rubra.* **c.** Two physiological castes: physiological differences maintained over time and with no morphological differences, e.g. *Monomorium pharaonis.* **d.** Physiology diverges over time forming physiological castes with no morphological differences, e.g. *Ectatomma tuberculatum.*

for physiological correlates, we should perhaps focus first on finding the physiological basis of observed behavioural specialisations, and then, if appropriate, look for morphological and age group correlates of these. Here I review physiological differences among age-related and morphological castes, showing that physiology can be as or more important to caste identity than morphology or age. I also give some examples of possible purely physiological castes.

## Morphological castes

Where morphological (or physical) castes occur, the size or shape of workers is correlated with the tasks they perform. Morphological castes are found in the termites and some ants. Although morphological castes are characterised by features of the exoskeleton, the differences between these castes often extend below the exoskeleton to the gland morphology and secretions (Fig. 1a). There are many examples of such physiological correlates of morphological caste. Where a particular morphological caste carries out most of the trail laying, the appropriate gland may be larger in that group, for example the enlarged Dufour's gland in the trail-laying *Pheidole fallax* minors, compared to the non-trail-laying majors (Law et al., 1965), and the proportionally longer poison-sac in the trail-laying intermediate-sized *Atta sexdens* workers compared to the other castes (Wilson, 1980). In other species, the specialisation is not gland size but rather the secretion produced. In the harvester ant *Messor barbarus*, the trail substance produced from the Dufour's gland of the media workers has the most potent recruitment effect, although it is major workers which have the largest Dufour's glands (Heredia and Detrain, 2000). In the termites too, trail laying ability may differ between castes in terms of the trail substance produced in *Nasutitermes ephratae* and *N. corniger* (Arab et al., 2006), or in the ability to produce any trail substance at all in *Trinervitermes bettonianus* (Leuthold and Lüscher, 1974).

A soldier (or major) caste defending the colony is one of the commonest morphological specialisations, and physiological correlates are widespread here too. In some ants, majors have larger poison glands than minor workers and produce all or most of the alarm pheromone (Law et al., 1965; Heredia and Detrain, 2000). Among the leaf-cutter ants, the composition of the alarm pheromones from the mandibular glands differs between soldiers, medias and minors (Do Nascimento et al., 1993; Hernández et al., 1999; Hughes et al., 2001; Francelino et al., 2006) and it also differs between majors and minors in the weaver ant *Oecophylla longinoda* (Bradshaw et al., 1979). In the nasute termites, the soldiers differ greatly in their physiology from other workers. The soldiers possess a specialised nasus for secretion of viscous defensive substances unique to the soldier caste (Miura and Matsumoto, 2000; Hojo et al., 2005). In other termite groups, the soldiers also show differences in the mandibular gland physiology (Miura et al., 1999).

In the leaf-cutter ants, the very smallest individuals specialise on tending the fungus garden. Substances which inhibit bacteria and alien fungi are produced from the metapleural glands. These glands are proportionally largest in the smallest workers, which makes them more resistant to parasitic fungi (Wilson, 1980; Poulsen et al., 2006). The small leaf-cutter ants also carry out brood care, and correspondingly have the proportionally largest postpharyngeal gland, from which larval food is secreted (Wilson, 1980). In the macrotermite *Macrotermes bellicosus,* labial gland secretions (important in trophallaxis

and nest construction) and gut enzymes differ between majors and minors (Hinze et al., 2002). It is clear that physiological specialisations within a morphological caste system have evolved many times in the social insects; indeed the morphological and physiological traits probably coevolved, and thus the physiological traits may be as important as the morphological traits in determining such caste differences.

## Temporal castes

Temporal (age-related) castes are more common than morphological ones, and are found in many bees, wasps, ants and termites. They vary in strength and discreteness, but generally follow the pattern of younger individuals working inside the nest, and older ones outside. The clearest examples of stable age-related or temporal castes are accompanied by physiological changes (Fig. 1b), so it has been suggested that temporal castes should be viewed as temporary physiological castes (Johnson, 2003). Physiological changes have been best studied in the honey bee *Apis mellifera.* In the honeybee, juvenile hormone (JH) increases during a bee's life and the yolk protein vitellogenin decreases. These changes are more closely linked to task than absolute age, as demonstrated by the low JH and slower decrease of vitellogenin in long-lived 'winter bees' which do not forage (Fluri et al., 1982). In addition, precocious foragers and over-aged nurses have JH and vitellogenin levels more appropriate to their task than their age (Fluri et al., 1982; Robinson et al., 1989; Huang and Robinson, 1992; Amdam et al., 2005). Both JH and vitellogenin influence the timing of the switch to foraging (Sullivan et al., 2000; Nelson et al., 2007). JH and vitellogenin exert regulatory influence on each other (Rutz et al., 1976; Pinto et al., 2000; Guidugli et al., 2005), and, at least in honeybees, changes in levels of these factors underlie many of the age-correlated physiological changes discussed below.

As with morphological castes, changes in glands correlated with age group are common, and many of these have been demonstrated to be correlates of age-related task, rather than simply part of the aging process. Younger honeybees, which care for brood, secrete a larval-feeding substance from well developed hypopharyngeal glands, which degenerate later in life (Kubo et al., 1996; Ohashi et al., 1997) This degeneration is caused by increasing levels of JH (Jaycox et al., 1974; Rutz et al., 1976). Hypopharyngeal gland degeneration will be reversed in some foragers if young bees are removed from the colony, showing the link with task (Van der Blom, 1993). Such 'reverted' bees show reduced JH and increased vitellogenin compared to same-aged foragers (Amdam et al., 2005). Changes in the composition of mandibular gland secretions with age are also seen in the stingless bee *Scaptotrigona postica* (Gracioli-Vitti et al., 2004) and the ant *Myrmica rubra* (Cammaerts-Tricot, 1974). In the termite *Macrotermes bellicosus* labial gland secretions (important in trophallaxis and nest construction) and gut enzymes change with age as workers move from feeding on plant material to feeding on fungus comb (Hinze et al., 2002). Reproductive physiology may also change with temporal caste, because in many species of social insect the workers produce non-viable trophic eggs to feed brood. In the wood ants *Formica sanguinea* and *F. rufibarbis*, the ovarioles are developed in younger workers, but degenerate in older workers (Hohorst, 1972; Billen, 1982).

Older workers, often foraging outside of the nest, have different glandular physiology from younger workers. In the honeybee, the now much reduced hypopharyngeal gland switches to secreting carbohydrate-metabolising enzymes required for the processing of nectar into honey (Kubo et al., 1996; Ohashi et al., 1999; Deseyn and Billen, 2005). In trail-laying ants, changes in the abdominal glands are common with age. In *Myrmica rubra*, the Dufour's gland which produces trail pheromones increases in size over the age period 0–17 days and, as the ant ages further, the secretions continue to increase in attractiveness (Cammaerts-Tricot, 1974). In *Tetramorium aculeatum* young workers have almost empty Dufour's glands, and the trail substance produced from their poison and sternal glands elicits less effect than that of the older foragers (Cammaerts et al., 1994). In the ant *Camponotus obscuripes*, formic acid reservoirs in the older foraging ants are a different shape and contain much more formic acid (used in alarm) than in younger nest workers (Fujiwara-Tsujii and Yamaoka, 2006).

In addition to differences in glandular physiology, foragers may be leaner, a pattern seen in bees, wasps and ants (O'Donnell and Jeanne, 1995; Blanchard et al., 2000; Toth and Robinson, 2005). In the wasp *Polybia occidentalis*, lipid stores decrease after performing their first external task (O'Donnell and Jeanne, 1995) whereas in the honeybee, lipid declines prior to the onset of foraging, and this decline has been demonstrated to have a causal role in the switch (Toth et al., 2005). Although external nest workers are older individuals, and older individuals have less lipid, in both these studies there was a closer correlation between task and lipid than between age and lipid (O'Donnell and Jeanne, 1995; Toth and Robinson, 2005).

Changes in brain physiology, both anatomical and chemical, can also be associated with temporal division of labour. Neuroanatomical changes usually involve the mushroom body; for example in honeybees, there are changes in mushroom body structure, visual input region and olfactory glomerular volume with temporal caste (Coss et al., 1980; Withers et al., 1993; Durst et al., 1994; Farris et al., 2001). Some of these are not just age-related changes in physiology, because precocious foragers show the same neuroanatomical patterns as normally aged foragers, and over-aged nurses do not progress to the full forager pattern of mushroom body structure (Withers et al., 1993; 1995). Mushroom body structure changes with age-associated task are also seen among wasps (O'Don-

nell et al., 2004) and ants (Gronenberg et al., 1996; Seid et al., 2005; Kühn-Bühlmann and Wehner, 2006). Neurochemical correlates of age are seen in the ant *Pheidole dentata* (Seid and Traniello, 2005) and the honeybee (Wagener-Hulme et al., 1999). In the honeybee, some of these changes are associated with task (Wagener-Hulme et al., 1999) or transitions between tasks (Schulz and Robinson, 1999; Schulz et al., 2002) and are modulated by juvenile hormone (Schulz et al., 2002). In the honeybee, hormone receptors in the ecdysteroid signalling pathway are expressed most strongly in the mushroom bodies of foragers (Yamazaki et al., 2006), though it has not yet been determined whether this change is age- or task-linked.

## Physiological castes

It is evident that physiological differences between castes are common, but are they always age-linked or connected to morphology? The possible existence of purely physiological castes is rarely mentioned. Hölldobler and Wilson (1990) suggest insemination as a physiological state which could define a caste but, in addition to reproductive physiology, the other physiological differences outlined above (glandular morphology, secretory products, leanness, neuroanatomy, neurochemistry) could also occur within same-aged monomorphic groups (Fig. 1c).

A recent paper on the monomorphic Pharaoh's ant, *Monomorium pharaonis* describes just such a case (Jackson et al., 2007). Within the Pharaoh's ant, only some ants are able to detect pheromone trails laid the previous day. These specialist 'pathfinders' retain their specialisations over time and are physiologically different from other foragers, as pathfinders have significantly lower ratio of monomorine 3 to monomorine 1 than other ants (Jackson et al., 2006). The proportion of the ants which are behaviourally and physiologically pathfinders remains constant in different age cohorts, suggesting that no age polyethism is involved here (Jackson et al., 2007). Venom in Pharaoh's ants is synthesised before eclosion of pupae (Jackson et al., 2007), so the consistency throughout age groups suggests that this group of specialists are developmentally determined, like morphological castes. As is also the case with most morphological castes, a level of behavioural flexibility is maintained in this physiological caste. Food deprivation temporarily increased trail-detecting performance in non-specialists, but it dropped again after feeding (Jackson et al., 2006).

In the Pharaoh's ant, the physiological caste seems to be stable across all age groups; however physiological specialisations also occur within an age group (Fig. 1d). In the ponerine ant *Ectatomma tuberculatum* there are changes in reproductive and glandular physiology with age, but also with task within same-aged cohorts. Workers specialising in brood care have more developed ovarioles (allowing them to lay trophic eggs) than other same-aged ants (Fénéron et al., 1996).

Physiological changes with temporal caste in honeybees have been well studied, as discussed above, and here too physiological specialisations within age groups have been recorded. Honeybee nurses have more developed ovaries and smaller poison glands than same-aged nest maintenance specialists (Huang et al., 1994). Wax-workers come from a particular age group with active wax-glands (Muller and Hepburn, 1992), but wax-working specialists also have lower Juvenile Hormone and higher dopamine levels than other members of this age group such as guards or food storers (Huang et al., 1994; Wagener-Hulme et al., 1999). Among older honeybees, foragers and soldiers differ behaviourally and genetically (Breed et al., 1990). There may be slight differences in age between these two groups (Wagener-Hulme et al., 1999) but the significant differences in hypopharyngeal glands and neurochemistry make the soldier caste more clearly defined by physiology than age (Huang and Robinson, 1996; Wagener-Hulme et al., 1999).

It seems likely that there may be many more such physiological castes throughout the social insects, but these may have been overlooked because physiological differences are less easily observable than morphological, age-related and behavioural differences.

## How would physiological castes arise?

Two types of physiological castes have been observed (Fig. 1). The physiological differences in the Pharaoh's ant are stable across all age groups. This sort of caste could arise due to differences in hormone levels or trophic factors during larval development, as morphological castes do. In this case, the physiological caste would be fixed before eclosion as is the case for morphological castes in ants. The second sort of physiological castes only diverge at certain stages of life, as in the honeybee and *E. tuberculatum.* These could arise in several different ways, as is the case for temporal castes. If individuals are initially identical, physiological task fixation could occur, amplifying differences which have arisen due to social interactions or spatial location (Franks and Tofts, 1994). Alternatively, genetic differences between individuals could lead directly to specialisation via an intrinsic physiological bias towards performing a certain task. Genetic differences could also lead indirectly to physiological bias via effects on spatial location or social clustering. Genetic differences between individuals specialising on different tasks have been recorded in bees, wasps and ants (Frummhoff and Baker, 1988; Robinson and Page, 1988; Stuart and Page, 1991; O'Donnell, 1998). Page et al. (2000) bred strains of bees which differ in their propensity to store pollen, and this behavioural difference during foraging is associated with life-long physiological characteristics. In 'high strain' bees which store more pollen, vitellogenin increases more rapidly in the young workers and declines more rapidly in older bees (Amdam et al., 2007). Thus genetically determined

differences in the timing of endocrine signals can have far-reaching effects on physiology and behaviour.

I suggest that physiology is an important aspect of caste, not only in its contribution to age-related and morphological castes, but also in its own right as a caste grouping factor. Indeed physiological differences (current or developmental) could be seen as the overarching caste grouping factor, while differences in morphology and age may be the observable signs. Behavioural specialisations may be flexible, and looking for physiological differences would help distinguish between stable castes and short-term behavioural specialisations. Age and morphological differences have been used for this purpose in the past, however while age and morphology make caste structures accessible for study, we should be prepared to look for more cryptic physiological castes, which may play just as important a role in division of labour.

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